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SIMULATING LINEAR FOREST DYNAMICS IN GREAT PLAINS ECOSYSTEMS UNDER CHANGING CLIMATES

by

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ABSTRACT. Individually-based, spatially-explicit gap models that simulate the effects of environmental change on the forest growth and succession have been well-developed and broadly used. However, most of these models are not suitable for the highly fragmented linear forests in the agroecosystems where forests are a minor but ecologically important component of the landscape. In this study, we used SEEDSCAPE, a moderately modified gap model designed for cultivated landscapes of the Great Plains, to simulate the effects of global change on the dynamics of linear forests. We simulated the forest dynamics under different climatic scenarios using current climate data and general circulation models (GCM). We simulated the agroecosystem with both riparian zones and shelterbelts that had very different water regimes, different widths, and initial species richness. Results showed that warming climates reduced community biomass in the linear forests, especially in shelterbelts. Linear forests with higher initial planting species richness and smaller width produced higher biomass per unit area. This modified model presents the first example of using spatially explicit, individual-based forest gap models to the largely fragmented linear forest types in the region. The model showed promise in applications and will serve as the valuable starting point for modeling biological diversity and forest succession in human-dominated landscapes of the Great Plains under changing climates.

INTRODUCTION

Human-dominated agricultural ecosystems in the Great Plains may be especially sensitive to future climate change because of its flat and highly fragmented nature. In the Great Plains, woody areas, usually riparian zones and shelterbelts, comprise only a small portion of the agricultural landscape but they play important roles in crop production through their sheltering effects and in providing habitats or corridors for plants and wildlife in cultivated areas (Fig. 1a). The establishment and growth of the linear forests will influence crop production and plants and wildlife conservation. However, The growth and succession of these Great Plains forests have been largely overlooked and little information on temporal changes in community structure is available.

Individual-based, spatially explicit gap models that simulate the effects of climate change on the forest growth have been well-developed and broadly used (e.g., Botkin 1993, Liu and Ashton 1998). In these models, the establishment, growth, reproduction, and death of individual trees on a small plot of land (e.g., 10 x 10 m) are simulated, and in many studies, the forest dynamics are assumed to represent the surrounding forest. Since these models were designed for continuous upland forests, direct application to the highly fragmented linear forests in the Great Plains presents a number of problems.

For forested regions in which a single plot is assumed to represent a large area, gap models usually include ubiquitous seed dispersal (i.e., where the plot receives seeds of all species that might occur in the landscape). Establishment of trees is entirely dependent on the survival of seedlings rather than on their arrival on the plot. In reality, the location of any plot in the landscape will affect its probability of receiving seeds that disperse from other plots in the

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landscape. Therefore, a single plot cannot be assumed to represent the entire forest accurately (Liu and Ashton 1998, Easterling et al. in press).

Linear forests result in a greater proportion of trees in the landscape that are on the forest's edge. Here they are likely to experience greater light availability and a different microclimate than interior trees. In addition, the Great Plains comprises a mixture of upland and riparian forests which experience very different water regimes. In upland areas in many parts of the Great Plains, the water table is extremely deep, and trees gain their water predominantly from precipitation. In riparian areas, water is also available from groundwater and adjacent streams or rivers. The availability of this water will fluctuate over time.

To accommodate the unique features of linear forest growth in agricultural landscapes, we developed a new model, SEEDSCAPE (Guertin et al. 1997). Based on existing gap models, this model was constructed to overcome the limitations of existing forest models, and to provide a starting point for understanding ecological processes in these heavily human-dominated landscapes. One important question is what are the ecological implications of future climate change and varying the dimensions of these linear forest corridors. Warming climates are likely to change the existing forest structure and dynamics and the linear forests with different widths may support different biodiversity values and crop productions.

In this paper, we use SEEDSCAPE to simulate the dynamics of riparian zones and shelterbelts with different species richness and widths and under different climatic scenarios. The goal is to develop design criteria for woody corridors' establishment and management in terms of their ideal size (length and width), spatial arrangement, and optimal density that can better balance crop production and biological conservation. We ask the following questions: (1)

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How will global climate change affect the growth of linear forests in the Great Plains? (2) How does forest width affect community biomass and evenness? (3) How does planting species richness affect the forest growth under different climatic scenarios?

THE *SEEDSCAPE* MODEL

The SEEDSCAPE model is derived from a gap model, JABOWA II (Botkin 1993). It simulates forest dynamics by monitoring the growth of individual trees as a physiological response to competition, temperature and CO_2 concentration and the availability of light, nutrients, and water under a changing climatic scenario in a spatially explicit landscape. The main features of the present SEEDSCAPE model include:

(1) Extension of the single-plot approach to an entire landscape of multiple plots (10 x 10 m^2) over a 100 x 100 grid (1 km^2; Fig. 1b). This can incorporate the fundamental differences between forest stands with small edge-to-area ratios (e.g., large forested tracts) and ones with large edge-to-area ratios (e.g., riparian forests). In addition, because the 1 km^2 landscape is not a closed system, plots along the edges of the landscape can be designated as seed sources. These plots contain species that are found outside the 1 km^2 landscape, but are close enough to deliver seeds to the landscape. Within this landscape, each plot is assigned particular values for soil type, initial vegetation, and whether the plot is in a riparian or upland location. The soil type determines moisture capacity, available nitrogen in the soil, soil depth and the depth to the water table. Initial vegetation determines whether the plot is cultivated and therefore incapable of supporting trees, or wooded. The species and diameter of all trees on each wooded plot are assigned at the start of the model run.

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(2) Allowing seed dispersal among all plots in the simulated landscape (each species can have up to three dispersal mechanisms within a total of eight dispersal categories) linking the entire array of species that occur in a given area and connecting all simulated plots. SEEDSCAPE uses the dispersal algorithm from the SEEDFLO model (Hanson et al. 1990). In this algorithm each plot is used as a potential seed source if it contains trees large enough to produce seed and if those trees actually produce seeds in a given year as determined by the species-specific probability of seed production. Initially each tree's age is set to the minimum age for seed production unless explicitly set to another age. For each tree on each plot, the probability of seeds reaching each of the other potentially wooded plots in the landscape is determined by the simple distance-decay function, $P_{ij} = d_j^{-\varphi}i$, where i is a species-specific dispersal agent, P_{ij} is the probability of a seed dispersing to plot j given a dispersal agent i, d_j is the distance in meters to plot j, and φ_i is the dispersal parameter for a dispersal agent i (Okubo and Levin 1989). Once seeds have arrived on a plot, the seedling establishment, growth, and mortality are similar to other existing gap models. The specific equations in SEEDSCAPE are the same as those in JABOWA-II (Botkin 1993).

(3) Locally variable water tables: For upland plots, the availability of water is the same as in JABOWA-II, and is determined by precipitation and by the water table. Because the water table in our study areas is extremely deep in upland locations, it is not normally a factor in tree growth. In riparian plots, however, the soil may be completely saturated due to a shallow water table resulting from flooding along water courses following precipitation events. SEEDSCAPE therefore allows for variable local water tables in riparian plots. The water table varies with water volume in the streams, which is in turn a function of runoff from surrounding agricultural

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fields. SEEDSCAPE uses the curve number method developed by the USDA-Natural Resources and Conservation Services (USDA-NRCS 1972) to calculate runoff volume following precipitation events.

STUDY SITE AND FIELD DATA

Field study was conducted in the forest corridors about 20 m wide at Mead, Nebraska which are typical of those found in the eastern and central Great Plains. The focal 1 km^2 landscape includes riparian zones along a drainage slough, planted shelterbelts, and crop fields. The southern half of the forest corridors within the landscape was cleared in 1971 and the northern half was cleared in 1979. Totally 25 tree and shrub species were found in the study area. Field data were collected from existing vegetation in 1995 from five 10 x 10 m plots along the corridor length. None of the survey plots contained all 25 species found at the study site. The number of stems of each tree species and diameter (DBH) of all trees were recorded, and a visual survey was made of the surrounding area to estimate the number and diameter of the potential seed source trees there. Twelve species were in the 1 km^2 landscape including the seed source plots and 10 of these species were found in the riparian strip. The forest corridors were initialized to have no woody vegetation at the start of the simulations.

Five iterations of a 400-year simulation for both shelterbelts and riparian zones with three different corridor widths (10, 20, and 30 m) were simulated under both current climatic conditions and RegCM2 climatic change scenarios. RegCM2 is a regional climate model developed by National Center for Atmospheric Research (NCAR; for details, see Giorgi et al. 1993a, b). Monthly weather data were obtained for 1967-1995 from the nearest weather station

near Mead, Nebraska. Soil types were determined from Saunders County soil survey maps.

We made cross-comparisons in total biomass and community evenness between: (1) current climatic conditions and global warming scenarios; (2) three corridor widths (10, 20, 30 m with total planted areas kept the same); (3) a species rich community (10 spp.) and less a diverse community (4 spp.). Finally, we simulated the population dynamics of each individual species under these different conditions.

SIMULATION RESULTS

It took 70-80 simulation years for both riparian zones and shelterbelts to reach a steady state under both current climatic conditions and climatic warming. After that biomass and species composition kept relatively constant over the other 320 simulation years.

Effects of climatic warming:

Given a certain level of species richness or width, the linear forests produced significantly lower biomass under warming climatic scenarios than under current climatic conditions (Figs. 2, 3, 4). This was especially remarkable in planted shelterbelts (data not shown). There was no evidence that climatic warming would cause greater spatial variation in biomass among simulated plots (Figs. 2, 3) but climatic warming did cause greater variation in biomass (or higher dominance) among component species (Fig. 5 vs. Fig. 6).

Effects of species richness

Linear forests with lower species richness (4 spp. vs 10 spp.) produced less biomass but

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resulted in higher spatial variation in biomass among simulated plots (Fig. 4; Fig. 2 vs. Fig. 3). However, there was no clear evidence that higher species richness could lead to lower spatial (among simulated plots) and temporal (among simulated years) variation in community biomass. The linear forests with higher species did produce higher biomass and higher community evenness under both current and warming climates (ANOVA, $P < 0.01$).

Effects of corridor width

Given the total forested area (many narrower corridors or fewer wider ones), significant effects of linear forest width on total biomass were detected (paired t-test, $P < 0.05$) but the spatial variation in biomass across simulated plots was smaller in wider corridors than in narrower corridors (t-test on standard deviation of biomass among plots; $P < 0.05$). We did not see any clear evidence that corridor width affected community evenness (paired t-test, $P > 0.05$). Forest width did not have any significant effects on the performance of individual species. Although the trajectories of each species were somehow different in narrower (10 m) and wider corridors (20 m), there were no significant differences in the relative importance of each species measured by biomass (data not shown).

The forests with higher species richness (10 species) showed great differences in biomass among the forests with different widths than those with only four species (Fig. Xx).

Another notable change was the difference in the switches of species dominance when the forests were designed with different widths, even though the forest species composition was still the same. For example, ... (Data not shown).

Responses of individual species

Among the 10 species (Table 1) used in our simulation for riparian zones under both current climate conditions and warming trends, *Prunus americana* showed a dramatic decline, especially under warming climate. Following the decline of *Prunus americana*, *Acer negundo* and *Morus alba* showed similar trends with the former dominating in the first 130 simulation years. After that period, both species declined with *M. alba* almost totally eliminated from the local community, but *Fraxinus pennsylvanica* then became the most dominant species, followed by *A. negundo* and *Populus deltoides* (Fig. 5).

In the shelterbelt with four species only, the patterns were different. *P. americana* and *M. alba* exhibited similar patterns as in riparian zones. But *A. negundo* became the dominant species after the first 10 simulation years and then continued its dominance, with its biomass keeping relatively constant over time. Under normal climatic conditions, *P. americana* and *M. alba* still kept their minimum existence over time, however, under warming climates, both species were eliminated from the local community after 20 and 150 years, respectively (Fig. 6).

DISCUSSION

The modified model, SEEDSCAPE, presents the first example of using spatially explicit, individual-based forest gap models to simulate successional processes in the largely fragmented linear forest types (riparian zones and shelterbelts) of the Great Plains. Although our results are still preliminary, the outcomes from our simulations suggest that the model performs reasonably well. It successfully detected the potential effects of global climate change on biomass and community evenness in both riparian zones and shelterbelts. The model also successfully

revealed the switches in species dominance under different climatic scenarios over time and the highly individualistic responses of the different species.

The application of SEEDSCAPE is to test the effects of climate change and forest corridor widths on the growth of component species in order to better select species and arrangements of these forest types in agroecosystems of the Great Plains. In this study, there is no evidence that wider corridors support higher plant community evenness. One reason could be that the model does not simulate all species that can potentially occur in these systems, which is still one of the weakness of the current SEEDSCAPE model (see below). The small differences in importance values between the smaller corridor widths (10, 20, 30 m) suggest that light penetration into the interior of the corridor does vary significantly at these widths.

Using different GCM models to examine the effects of global climate change would certainly produce different results. Using the regional climate model, RegCM2 (see Giorgi et al. 1993), our simulation results indicate that lower biomass and community evenness would be produced regardless of the original species richness and forest shape (i.e., width). However, it is not yet clear at this time from our model structure why spatial variation (standard deviation) in biomass across simulated plots became greater after 225 simulation years in the linear forests with 10 species under both current climate and warming climate (Fig. 2).

Our simulation results support results from earlier studies that demonstrated a richer community would produce higher biomass and community evenness. However, there was no clear relationship between species richness and community stability (measured as CVs on biomass over time) in our simulation results.

Based on the assumptions and procedures used in this research, the results suggest that

simulated changes in the forest corridor width of Great Plains do have a significant effect on successional characteristics of those forests until the widths become quite large. We infer from these results that a trend toward protection of these forest strips leading to the growth of forest widths to much greater than 20m???? may have significant effects on community structure.

There are some weaknesses in the SEEDSCAPE model: (1) Feedbacks between trees and environment have not yet been incorporated into the model (forest growth itself will modify the local and regional environments; see Chen et al. 1999); (2) Under-story species are not yet considered. The present model only includes trees and dominant shrubs. This is a result of two factors: First, too expensive in terms of computing (time and space), and second, not enough empirical data are available. Ideally all component species in different plant life forms (i.e., shrubs and herb species) should be included in future modeling improvement. This would require a design of smaller patches for shrubs and herbaceous plants nested within the original large patches for trees.

Wooded corridors are expected to expand throughout much of the Great Plains because of planting, suppression of wildfire (Knight et al. 1994), and reduced river flows in some riparian areas (Johnson 1994). Future revisions of the model focusing on the expansions of forests over time, dispersal abilities, and the spatial configurations of riparian zones and shelterbelts across the agricultural landscape to the regional level are critically needed.

In summary, SEEDSCAPE model provides a feasible method for increasing our understanding of forest succession in Great Plains agroecosystems. Our simulation results showed that the structure and dynamics in the linear forests (riparian zones and shelterbelts) were significantly different under different climatic conditions. Forest design (i.e., planting

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species richness and width) and management practices can significantly affect future forest structure and dynamics. This modified model presents a good example of using spatially explicit, individual-based forest gap models to the largely fragmented linear forest types in the region. It shows promise in various applications and will serve as a valuable starting point for modeling biological diversity and forest succession in human-dominated landscapes of the Great Plains.

ACKNOWLEDGMENTS

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Table 1. Species-specific reproductive parameters and dispersal agents. SAP is the max. # saplings added per year. Age_{min} and Age_{max} are the minimum and maximum ages at which a tree can produce seeds. $Pr_{(seeds)}$ is the probability that a tree will produce seeds in a given year. Dispersal agents are based on Malanson and Armstrong (1996).

Species	SAP	Age_{min}	Age_{max}	$Pr_{(seeds)}$	Dispersal agent	
					Primary	Secondary
Acer negundo	3	30	100	1.0	1	
Celtis occidentalis	3	35	200	0.8	5	7
Fraxinus pennsylvanica	10	15	150	0.8	2	8
Juniperus virginiana	3	10	150	0.8	6	
Morus alba	3	5	125	1.0	6	
Populus deltoides	10	25	150	0.9	4	7
Prunus americana	60	10	40	1.0	5	7
Salix amygdaloides	10	10	85	0.9	4	
Ulmus pumila	15	15	70	0.5	2	
Ulmus rubra	3	15	200	0.5	2	

Table 2. Values of φ for each dispersal agent used in dispersal equation. Dispersal agents are based on Malanson and Armstrong, 1996.

Dispersal agent	i	φ
Wind (short distance)	1	1.07
Wind (intermediate)	2	1.04
Wind (intermediate)	3	1.01
Wind (long-distance)	4	0.90
Mammal	5	1.02
Bird (blue jay)	6	0.94
Bird (other)	7	0.99
Gravity	8	10000.00

FIGURE LEGENDS

Figure 1. The three major spatial components (riparian zones, shelterbelts, and crop lands) in the agricultural landscapes of the Great Plains (photo provided by G. Wells. Below: A fraction of the spatially explicit agricultural landscape (1 km²) simulated using SEEDSCAPE which contains 10,000 10 m x 10 m plots (Black: riparian zone, shade: shelterbelt, open: crop lands).

Figure 2. Temporal variation in biomass (vertical bars indicate the spatial variation of biomass among simulated plots) in the simulated forests with 10 species under both current and warming climates.

Figure 3. Temporal variation in biomass (vertical bars indicate the spatial variation of biomass among simulated plots) in the simulated forests with four species under both current and warming climates.

Figure 4. Comparison of temporal variation in biomass in the simulated linear forests with 10 and four species under both current climatic conditions and climatic warming.

Figure 5. Temporal variation in biomass of individual species in the simulated forests with 10 species under current and warming climates.

Figure 6. Temporal variation in biomass of individual species in the simulated forests with four

species under current and warming climates.

Biomass per 10m² versus Simulation year.

NORMAL

WARMING

Legend:
— A. negundo
− − F. pennsylvanica
− − M. alba
··· J. virginiana
−·−· Pr. americana
− − − U. rubra
− − Po. deltoides

The y-axis is labeled "Biomass per 10m²" and the x-axis is labeled "Simulation year". The top panel is labeled "NORMAL" and the bottom panel is labeled "WARMING".

Legend:
- A. negundo
- F. pennsylvanica
- M. alba
- J. virginiana
- Pr. americana
- U. rubra
- Po. deltoides

NORMAL

WARMING

Biomass per 10m^2

Simulation year

———— A. negundo   — — — — Morus alba
— — · — Celtis occidentalis   — · — · — Prunus americana